Fish Brains: Anatomy, Functionality, and Evolutionary Relationships

The Welfare of Fish

Kotrschal, Alexander; Kotrschal, Kurt

https://doi.org/10.1007/978-3-030-41675-1_6

Chapter 6
Fish Brains: Anatomy, Functionality, and Evolutionary Relationships

Alexander Kotrschal and Kurt Kotrschal

Abstract In this chapter, we provide an overview of the anatomy, functionality, and evolution of the fish nervous system. Our focus will be on the brain in the vertebrate group with the greatest variation in brain form and function, the actinopterygian bony fishes. We first describe central (CNS) and autonomic (ANS) nervous systems and then characterize the major distal components of the CNS (spinal cord, spinal nerves, cranial nerves), before we summarize the brain regions and their connections and highlight some similarities and differences between different fish taxa. The second part of this chapter is devoted to variation in fish brain anatomy, including a discussion of comparative brain anatomy evolution and brain plasticity. We finish with a summary of the evolutionary costs and benefits of brain size based on results in guppies (*Poecilia reticulata*) artificially selected for large and small brains. With respect to fish welfare, we conclude that their great brain diversity reflects the diverse cognitive needs of fishes. However, their lifelong high rates of neurogenesis should also make individuals capable to cognitively adapt to a certain range of environmental conditions.

Keywords Fish brain · Brain anatomy · Ecomorphology · Brain size · Artificial selection

A. Kotrschal (✉)
Zoological Institute, Stockholm University, Stockholm, Sweden

Behavioural Ecology, Insitute of Animal Sciences, Wageningen University, Wageningen, Netherlands
e-mail: alexander.kotrschal@wur.nl

K. Kotrschal
Department of Behavioural Biology, University of Vienna, Wien, Austria

Konrad Lorenz Forschungsstelle, University of Vienna, Grünau, Austria

Wolf Science Center, University of Veterinary Medicine, Ernstbrunn, Austria

6.1   Anatomy and Function of the Nervous System

The central nervous system (CNS) of vertebrates including fish consists of the brain and the spinal cord, linking with receptors and afferent organs via the motor and sensory nerves. Although most research is done on neuron properties and how they connect to each other a majority of cells in the CNS are of various other types. Glial cells, for instance, support the neurons physically, electrically insulate them, play a role in brain development and homeostasis, and may also be involved in information processing. Today we have a good understanding of how some anatomical arrangements function. Examples of especially well-understood systems are the Mauthner neurons governing a fundamental escape response, the electroreceptive system of mormyrid fishes, or the visual system in general.

6.1.1   The Central Nervous System

The CNS is arguably the most complex organ in any vertebrates' body. There are a large number of specialized cells, which are intricately connected, interacting with each other in diverse ways. In the following, we can only give a brief account of this complexity.

6.1.1.1   The Spinal Cord

The fish spinal cord is the phylogenetically oldest part of the CNS and hence, similar in structure to the spinal cords of all other vertebrates. During embryonic development, the CNS forms when neural folds roll in and fuse (Nieuwenhuys et al. 1998). In cross sections, the central area (with the cell bodies of the cord neurons) appears darker than the outer zone. Those areas are therefore called "grey matter" and "white matter", respectively. The white matter is mainly composed of ascending and descending fibres organized in distinct tracts: a dorsal somatic sensory tract, a lateral visceral sensory and visceral motor tract, and a large ventral somatomotor tract. In most fishes, the paired large axons of the Mauthner neurons descend in the ventral grey matter. Mauthner neurons are lacking in adult elasmobranchs (Bone 1977). They govern the C-start escape response (the"C" describes the typical body in the process of escaping) and function already early in ontogeny. Mauthner neuron axons decussate at the Mauthner chiasm; hence, when one cell is stimulated to fire, the C-start moves the head away from the aversive stimulus, which enables a very fast change of swimming direction. Mauthner neurons are the classic example of a hard-wired central nervous system response mechanism.

6.1.1.2   The Spinal and Cranial Nerves

Segmental dorsal and ventral nerve roots emerge from the spinal cord and, except for in lampreys, unite to form the spinal nerves, which carry motor, sensory, and autonomic signals between the spinal cord and the body. The ventral root axons of the spinal somatomotor neurons connect to the musculature, while the dorsal root contains the sensory neurons, connecting to the peripheral sensory systems. Whereas the bodies of the motor neurones form the ventral horn of the spinal cord grey matter, the sensory neurones are situated in segmental ganglia outside the cord (Fig. 6.1). Most of the cranial nerves follow the same basic pattern, but emerge from the rostral part of the spinal cord and the brain stem. They are numbered from rostral to caudal. The optic cranial nerve II deviates from this segmental arrangement pattern, as the eye develops via outpouching of the lateral neural tube (see below), and is, therefore, a brain-internal connection and should, therefore, be termed "tract" rather than "nerve". The olfactory nerve (I) connects the olfactory mucosa with the olfactory bulbs. If the bulbs are located directly at the mucosa, like in cyprinids, this is a brain-internal connection and therefore, called a "tract". The terminalis nerve conveys information from most rostral sensory systems; it is numbered 0, because it was described after the other nerves have already been numbered. The other cranial nerves (from front to back) are the oculomotor (III), trochlear (IV), trigeminal (V),
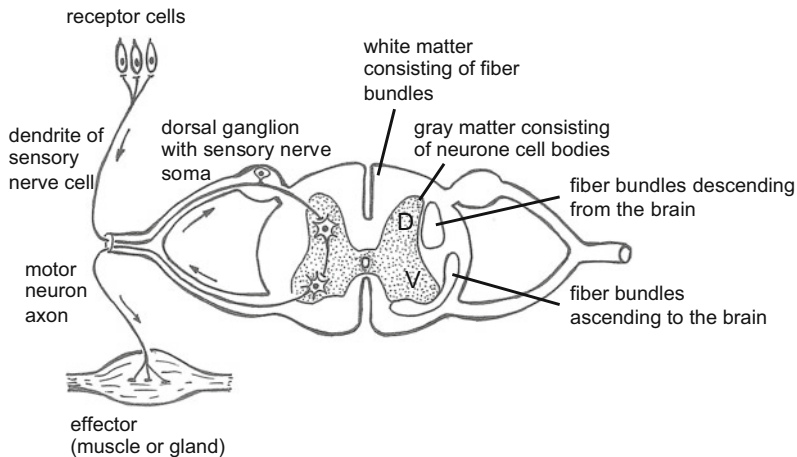
Fig. 6.1 Spinal cord and nerves (cross section) and their connections to sensory cells/organs and effectors. The central, butterfly-shaped grey matter consists mainly of nerve cells (D: sensory dorsal horn interneurones; V: ventral horn with motor neurones). Arrows give direction of potential conduction. The dendrites/axons of the sensory nerve cells, situated in the dorsal ganglia, are activated by peripheral receptors and transport the action potentials towards networks of interneurones in the grey matter, the output of which is communicated to the effectors via the axons of the ventral horn motor neurones. The local circuits of the spinal cord communicate with the brain via ascending and descending fibre bundles

abducens (VI), facial (VII), auditory (VIII), glossopharyngeal (IX), vagal (X), accessory (XI), and hypoglossal (XII) (Von Kupffer 1891).

6.1.1.3 The Brain

The brain is the enlarged anterior pole of the spinal cord, which has developed because also the major vertebrate sensory systems are located at the anterior pole of the body. For functional reasons, particularly the ventral brain areas are the phylogenetically most conservative structure; hence, its basic organization is grossly similar across all vertebrates, including fishes. However, owing to the diverse sensory orientation of fishes, the different regions can differ greatly in size and form. In fact, the fishes show the greatest variation of brain anatomy and brain function in all vertebrates (Nieuwenhuys et al. 1998). Figure 6.2 shows gross variation between the major groups of fish and Fig. 6.3 shows more detailed differences between the brains of two modern teleosts. The rostral spinal cord is continuous with the brain stem, with the ventral diencephalon as the most rostral pole, ending underneath the anterior commissure of the forebrain. Hence, the ventral brain composed of the modified rostral spinal cord; dorsally, it carries a series of prominent structures. During early ontogeny, the anterior end of the neural tube differentiates into neuromeres. Figure 6.4 shows how the three largest and most anterior neuromeres develop into the telencephalon, diencephalon, and the mesencephalon, while the seven more caudal neuromeres differentiate into the Rhombencephalon. From rostral to caudal, the three main regions are the forebrain (Prosencephalon), the midbrain (Mesencephalon) and the hindbrain (Rhombencephalon). The forebrain is divided into paired olfactory bulbs, ventrally attached to the telencephalic hemispheres, dorsally covering the Diencephalon (the "between-brain", consisting of Thalamus, Hypothalamus Subthalamus, Epithalamus, and Pretectum). Towards caudal, the midbrain roof is developed as paired optic lobes, followed by the Cerebellum (Metencephalon), dorsally attached to the Medulla oblongata (Myelencephalon) (Fig. 6.4; Nieuwenhuys et al. 1998; Northcutt and Davis 1983; Northcutt 1978).

The *brain stem* houses primary representation centres for all somatosensory faculties except olfaction and vision, and features a degree of variability hardly matched by other brain divisions. In unspecialized, evolutionary "mainstream" fishes, from agnathans to basic teleosts, neurone groups in the dorsal brain stem are arranged in four horizontal columns with sensory components of cranial nerves IV–XII and of two rostral and one caudal lateral line nerves terminating in the two dorsalmost columns, while motor fibres originate from ventrally located centres (Allis 1897; Webb and Northcutt 1997). The dorsal, sensory columns along the wall of the fourth ventricle process the senses of hearing, lateral line, and taste. Such somatotopic arrangement may facilitate the formation of short-loop reflexes (Kanwal and Finger 1992), and of sensomotory specializations such as the taste-dominated cyprinid palatal organ (Sibbing 1991). One additional, dorso-rostral column is found in fishes with the ability to process electrosensory information (e.g. in
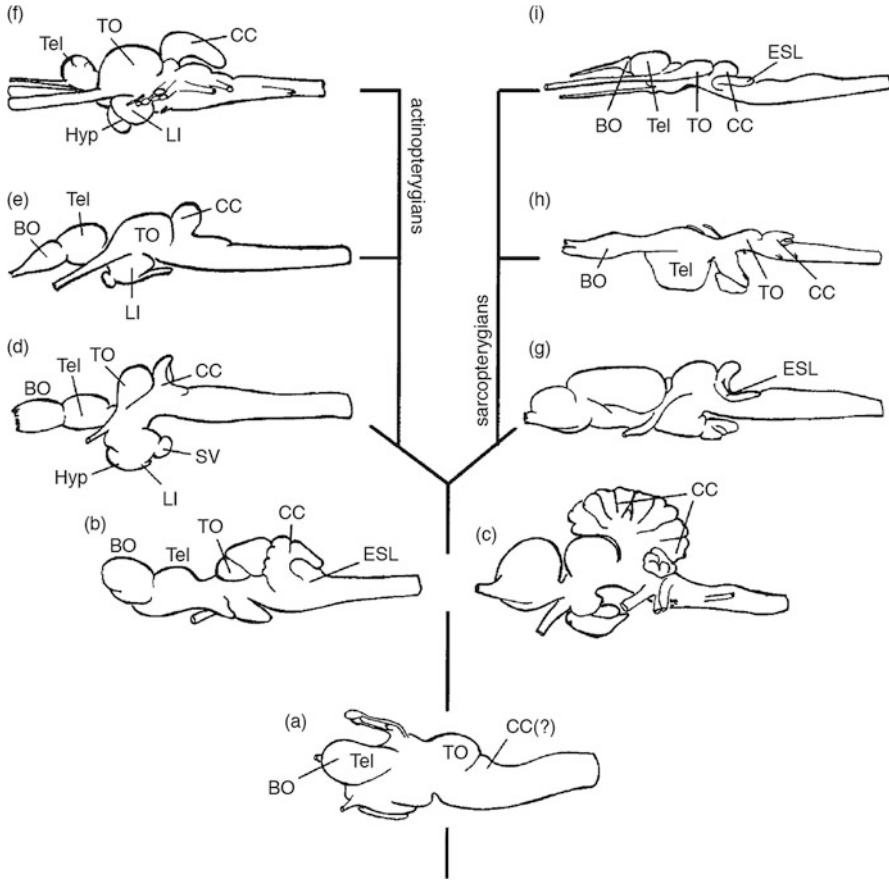
Fig. 6.2 Representative brains showing variation between major groups of fish. Forebrains are evaginated in lamprey (**a**: *Petromyzon*), in the elasmobranchs (**b**: *Acanthias*, **c**: *Cetorhinus*), lungfish (**h**: *Ceratodus*), and the coelacanth (**i**: *Latimeria*), but everted in the actinopterygian line, such as in the bichirs (**g**: *Calamoichtys*), sturgeons and neopterygians (**d**: *Acipenser*, **e**: *Amia*, **f**: *Gadus*). *BO* Bulbus olfactorius, *CC* Corpus cerebelli, *ESL* electrosensory lobe, *Hyp* Hypophysis, *LI* Lobus inferior, *SV* Saccus vasculosus, *Tel* Telencephalon, *TO* Tectum opticum. Brains are not to scale, reproduced with permission from Kotrschal et al. (1998)

Calamoichthys and *Latimeria*). The roof of the fourth ventricle is formed by a choroid plexus with varying degrees of differentiation (Weiger et al. 1988). Hypertrophy of areas within the dorsal column is associated with sensory specializations and these may form prominent bulges as in many carp- and cod-like fishes (Kotrschal et al. 1998). In addition to several ascending and descending fibre systems, the brain stem houses the reticular formation, a ventrally located system for basic maintenance and life support (Davis and Northcutt 1983).

The mesencephalic and diencephalic tegmentum continues rostrally to the brain stem with connective and integrative systems for brain structures arising from its
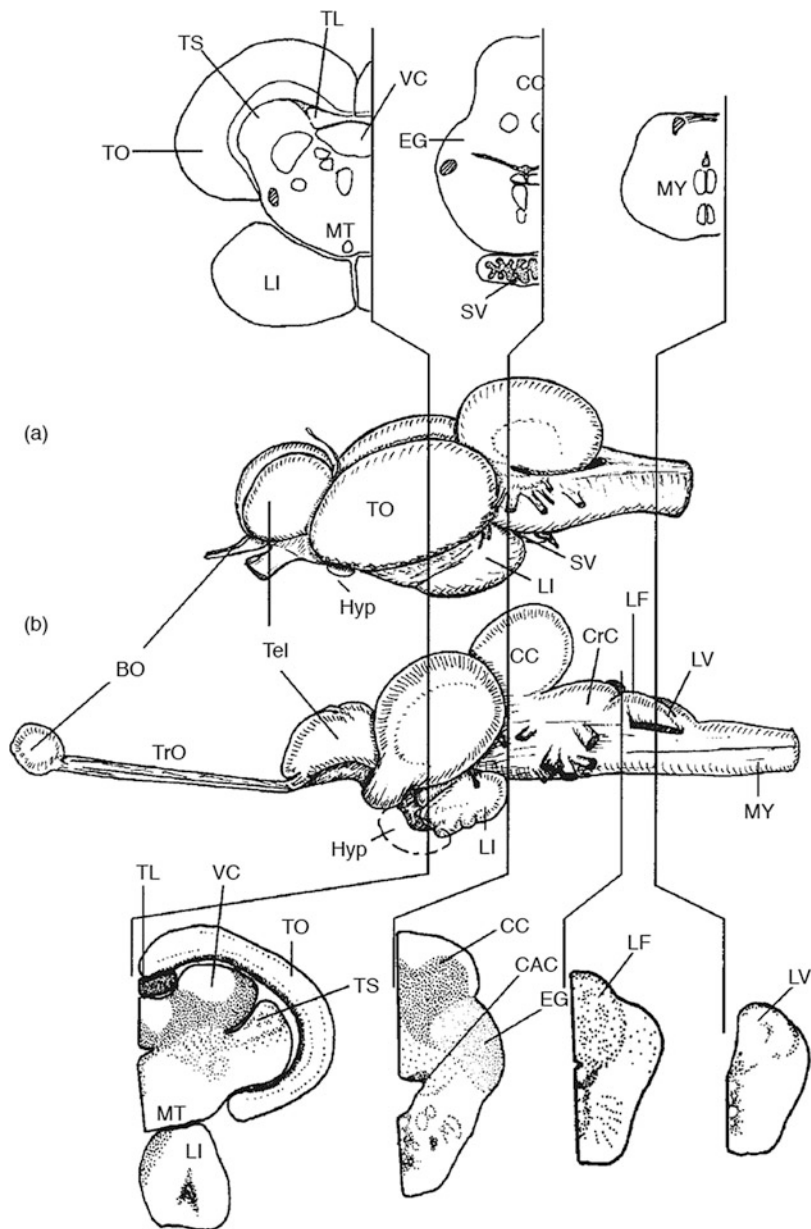
Fig. 6.3 Comparison between a perciform and a cypriniform brain: (**a**) blenny, *Blennius incognitus*; (**b**) roach, *Rutilus rutilus*. Lateral views in the middle of the page, representative cross sections at levels indicated by the vertical lines at top and bottom of the page. Note the small Bulbus olfactorius, but large Telencephalon, Tectum opticum, and Corpus cerebelli in the blenny. In the roach, the olfactory bulb is remote from the Telencephalon, and the somatosensory (taste) lobes of the brain stem, Lobus facialis, and Lobus vargus are large. *BO* Bulbus olfactorius, *CAC* Central acoustic area, *CC* Corpus cerebelli, *CrC* Crista cerebellaris, *EG* Eminentia granularis, *Hyp* Hypophysis, *LF* Lobus fascialis, *LI* Lobus inferior, *LV* Lobus vagus, *MT* Mesencephalic tegmentum, *MY* Myelencephalon, *SV* Saccus vasculosus, *Tel* Telencephalon, *TL* Torus longitudinalis, *TO* Tectum opticum, *TrO* Tractus olfactorius, *TS* Torus semicircularis, *VC* Valvula cerebelli. Redrawn after Kotrschal et al. (1998)

Fig. 6.4 Vertebrate brain ontogeny (mouse). Top: Early stage: The rostral (left) neural tube shows the appearance of the forebrain (F), midbrain (M), and hindbrain vesicles (H), with the developing spinal cord (SpC). Bottom: Later stage: More subdivisions appear. Forebrain: CSP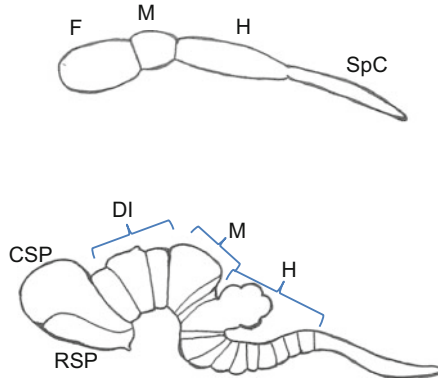: caudal secondary Prosencephalon; RSP: rostral secondary Prosencephalon; DI: prosomeres 1–3 of the Diencephalon; M: two mesomeres of the midbrain; H: isthmus region and hindbrain rhombomeres 1 to 11. Redrawn after Puelles et al. (2013)

roof: the Cerebellum, the Tectum opticum, and the forebrain (Davis and Northcutt 1983). Brain stem and tegmentum are continuous with each other and the sub-cerebellar secondary gustatory nucleus may serve as an arbitrary border. In a rostrocaudal direction, the tegmental third ventricle changes from a slit-like gap to a narrow channel before opening into the fourth ventricle. Several structures form as extensions to this ventricle. The inferior lobes of the Hypothalamus are paired, ventral diencephalic hemispheres specific to ray-finned fishes, serving as multimodal integration centres. In all vertebrates, the hypothalamic Tegmentum converts sensory inputs into hormonal and behavioural responses. In this context, the diencephalic and tegmental ventricle is lined by a number of "paraventricular organs", most of them equipped with cerebrospinal fluid-contacting neurons and distinctive ependymal cells as part of brain-internal humoral communication system based on the liquor. Ependymal cells line the ventricular cavities, they are one of the neuroglial cell types and are involved in the production of cerebrospinal fluid. Specific for the actinopterygian bony fishes is the saccus vasculosus (Fig. 6.2), an organ serving as a sensor of seasonal day length (Nakane et al. 2013). The hypothalamic Neurohypophysis serves as a central humoral command unit of physiology and behaviour. Dorsally, the choroid plexus of the third ventricle forms several extensions, such as the Saccus dorsalis with its light-sensitive and endocrine Epiphysis or other circumventricular organs.

The Cerebellum varies in extent from a small ridge in ancestral or sedentary, benthic fishes (Fig. 6.1) to a prominent structure in most modern teleosts (Fig. 6.2). Although relatively large in pelagic sharks or teleosts swiftly manoeuvring in 3D, it is not necessarily characteristic for a pelagic lifestyle per se (below). Particularly in modern electrosensory fishes, this structure may become massively enlarged,

covering the entire surface of the brain in *Gnathonemus* (Maler et al. 1991). Various cerebellar subdivisions serve a variety of functions including cognitive and emotional contexts (Rodríguez et al. 2005). Corpus and Valvula cerebelli, the latter as a rostral extension beneath the optic tectum, are intimately connected and appear to play roles in spatial orientation, proprioception, motor coordination, and eye movement. The central acoustic area forms as a granular area at the ventral Cerebellum, co-varying in size with the development of the peripheral hearing apparatus (Popper and Fay 1993). Inputs from the inner ear and from lateral line fibres terminate at the Eminentia granularis, a parvocellular area on both sides of the lateral corpus (Fig. 6.2). The Crista cerebelli, caudal and in continuation with the molecular layer of the corpus, predominantly processes lateral line input (Davis and Northcutt 1983).

The Tectum opticum (TO) as the mesencephalic roof consists of paired dorsal hemispheres with a cortex-like layering of grey and white matter, separated from the Tegmentum by ventricular spaces. The TO receives projections from contralateral retinal ganglion cells; it processes the primary visual input and participates in significant bidirectional communication with the brain stem (Davis and Northcutt 1983). Tectal development varies closely with eye size, visual orientation (Vanegas and Ito 1983; Zaunreiter et al. 1985), and lateral line dependence (Schellart 1991) and is also present in ontogenetically or phylogenetically blind fishes (Voneida and Fish 1984). The Retina ontogenetically forms as part of the Diencephalon and shows considerable structural variation related to phylogeny, ontogeny, ecology, or lifestyle (Kotrschal et al. 1998).

Below the optic lobes, the Torus longitudinalis extends into the sub-tectal ventricle as a pair of longitudinal cylinders (Fig. 6.2). Its presumed functions include postural control, detection of luminance levels, and monitoring of saccadic movement. Also, it has a role as premotor centre between Telencephalon and brain stem (Wullimann 1994).

The Telencephalon arises from the rostral portion of the embryonic neural tube forming two hemispheres. In more ancestral taxa of agnathans, elasmobranchs, and sarcopterygians these develop as in the majority of vertebrates, by the bulging out (evagination) of the lateral walls and therefore, contain a central ventricle. In contrast, the actinopterygian forebrain forms by bending out (eversion) of the dorsal walls of the embryonic neural tube (Nieuwenhuys 1982). Hemispheres are therefore solid, and a T-shaped ventricle extends up to the dorsolateral surfaces of the hemispheres and separates the two halves. Centrally, the two hemispheres are closely attached to each other and may even fuse. In addition to secondary olfactory fibres, which terminate throughout the entire structure, virtually all sensory modalities project into the dorsal Telencephalon through lemniscal pathways (Finger 1980); hypothalamic and primary olfactory input ascend from the ventral forebrain. The latter also contains the Commissura anterior with a peduncle of decussating fibre tracts for a two-way flow of information between the Telencephalon and Diencephalon as well as intra-telencephalic fibres. Fish with parts of their forebrains ablated feed, grow, and behave normally in most respects, but exhibit significantly

diminished rates of learning and do not engage in more complex social tasks (Salas et al. 2006; Portavella et al. 2002; Szabó 1973).

The bulbus olfactorius of all fishes evaginates from the rostral tip of the embryonic neural tube. Its ventricles are secondarily reduced or absent in advanced actinopterygians. Primary fibres from the olfactory mucosa terminate within glomerular structures of the olfactory bulb neuropil in a chemotopic way, i.e. fibres from olfactory mucosa neurons with similar receptor characteristics terminate within the same glomerulus. Large projection neurons, mitral cells, and tuft cells project into the Telencephalon and Diencephalon via medial and lateral olfactory tracts. In most species, the olfactory bulbs remain attached to the rostral telencephalon, but are attached to the olfactory mucosa in ostariophysean teleosts, connecting to the forebrain via a secondary olfactory tract. Figure 6.5 illustrates the phylogenetic change in brain regions emphasis across the fishes.

The nerve cell bodies (perikarya) of the Nervus terminals, located at the junction between olfactory bulbs and Telencephalon, send processes into the olfactory mucosa, the Diencephalon, and into most other brain areas including the Retina (Kotrschal et al. 1998; Nieuwenhuys et al. 1998). The function of this olfactoretinalis system was studied in medaka (*Oryzias latipes*). The terminal nerve gonadotropin-releasing hormone 3 (TN-GnRH3) neurons function as a gate for activating mating preferences based on familiarity. Basal levels of TN-GnRH3 neuronal activity suppress female receptivity for any male. Visual familiarization facilitates TN-GnRH3 neuron activity, which correlates with female preference for the familiarized male (Okuyama et al. 2014).

6.1.2   The Autonomic Nervous System

As part of the peripheral nervous system, the autonomic nervous system (ANS) composed of sympathetic and parasympathetic elements, governs all "involuntary" bodily functions. These fibres innervate smooth muscles, for instance around blood vessels, in the gut, spleen, urogenital tract, heart, and in teleost fishes also in pigment cells, and are vital for controlling homeostasis (Young 1931). Generally, the efferent fibres from central neurons are not directly connected with peripheral organs; they are rather linked via synapses to peripheral ganglion cells, which then innervate the target organ. Hence, the central nerve fibres are called pre-, the peripheral nerve fibres post-ganglion fibres. The autonomic nervous system in fishes is usually divided into the cranial autonomic, the spinal autonomic, and the enteric system of the gut (Bone et al. 1982). Teleosts, other fishes, and even other higher vertebrates differ from elasmobranchs in that the spinal autonomic ganglia are linked to the spinal nerves via branches carrying both pre- and post-ganglionic fibres. In teleosts, these also innervate skin melanophores (Mills 1932). Another difference lies within the vagal nerve (X) that in teleosts has both excitatory and inhibitory actions in the gut, while in elasmobranchs the vagus nerve does not control gut movements (Young 1980).

Fig. 6.5 Representative actinopterygian brains, in mid-sagittal view. Drawn from freshly perfusion fixed brains. All scale bars 5 mm. From bottom to top: *Acipenser ruthenus* (34.5 cm body length), *Amia calva* (20 cm), *Salmo trutta* (32 cm), *Tinca tinca* (16.5 cm), *Parablennius sanquinolentus* (13 cm). Note the amphibian brain-like features in the holostean (palaeozoic radiation of acinopterygians) and still, in the holostean (mesozoic radiation). Please also note the decrease in relative size, of the olfactory bulb (BO) and an increase in the size of the Telencephalon (Tel) towards the modern actinopterygian representatives. *BO* olfactory bulb, *Bst* brain stem, *Ca* anterior vommissure of the optic tract, *Cer* Cerebellum, *E/Sd* Epiphysis/Saccus dorsalis, *Hyp* Hypophysis, *Li* diencephalic inferior lobe, *Sv* Saccus vasculosus, *Tel* Telencephalon, *TO* optic tectum
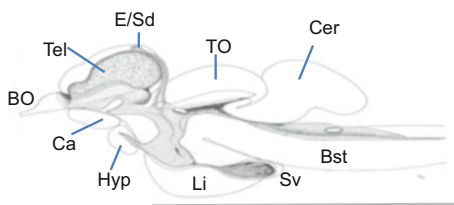
Teleostei, Perciformes,
Parablennius
sanquinolentus
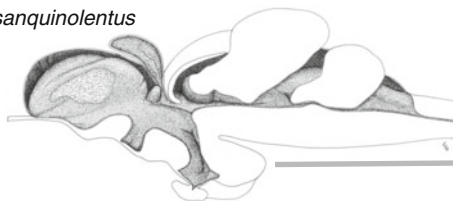
Teleostei,
Cypriniformes, Tinca
tinca
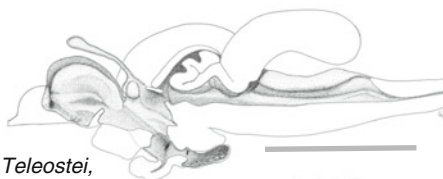
Teleostei,
Salmoniformes, Salmo
trutta

Holostei,
Amiiformes, Amia
calva

Chondrostei, Acipenseriformes
Acipenser ruthenus

6.2   Variation in Brain Anatomy

In most fishes, the brain is considerably smaller than the space available and may in some cases occupy only about 6% of the brain cavity in an elasmobranch (Kruska 1988). The excess space is commonly filled with lymphatic, fatty tissue. Nevertheless,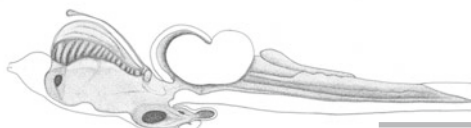 in Lake Tanganyika cichlids, skull morphometry seems to determine brain shape and constrain its evolution (Tsuboi et al. 2014a). Most neurons are relatively large in agnathans, sarcopterygians, chondrosteans, and elasmobranchs, but are small in teleosts. The apparent evolutionary decrease in cell size probably arises from size constraints during larval life, when, at only a few millimetre in length, teleost larvae are the smallest fully functional vertebrates (Kotrschal et al. 1990). Intergroup comparisons commonly based on brain size relative to body size can thus be misleading. Recent advances in using flow cytometry to quantify neuron numbers should prove useful in getting the story right (Herculano-Houzel 2009; Marhounová et al. 2019).

Brains scale negatively allometric with body size, with ontogenetically and phylogenetically small fish tending to have relatively large brains and vice versa (Brändstatter and Kotrschal 1990; Striedter 2005). There appears to be a coarse trend towards an increase in relative brain size during phylogenetic development. Agnathans, for example feature some of the relatively smallest brains, whereas those of perciforms are among the largest. The sexes generally show similar relative brain sizes with exception of the three-spined stickleback (*Gasterosteus aculeatus*), where, at similar body sizes, male brains are up to 23% larger than female brains (Kotrschal et al. 2012a). Possibly, this dramatic sexual size dimorphism is generated by the many cognitively demanding challenges that such territorial, parental males are faced with, including elaborate courtship displays, the construction of an ornate nest and a male-only parental care system (Östlund-Nilsson et al. 2007). Also, advanced courtship behaviour in cichlids (Kotrschal and Taborsky 2010) and demanding spatio-temporal orientation in females of some blennies (Costa et al. 2011) impact brain anatomy and size.

Faculties for sensory perception, central processing, and behavioural responses undoubtedly reside primarily within an organism's nervous system. The motor generators for the species-specific action patterns "innate behaviours" (Tinbergen 1951) reside in the spinal cord, whereas the brain is the command centre for selectively disinhibiting the motor generators for these action patterns in service of organized behaviour. In case of reflexes, a stimulus directly triggers a motor response via spinal cord circuits and the brain is informed only thereafter.

Adaptive radiation has produced a functional diversity of structures, shapes, and sizes rivalled by few other organs, unprecedented in non-fish vertebrates (Nieuwenhuys et al. 1998). A chief aim of evolutionary neurobiology and ecomorphology is to reveal how physical brains reflect sensory orientation, cognitive potential, and motor abilities. Viewed within a phylogenetic context, a study of this diversity can uncover how brains have adapted to the requirements of disparate habitats, ecologies, and behavioural needs. One century of ecomorphological

research (Herrick 1902, 1906) has produced a large empirical database for fish brains, which we attempt to briefly summarize here.

"Fish" is a collective term for more than half of all known vertebrate taxa. Embodying more than 400 million years of vertebrate evolution, taxonomic distance within this group is immense, greatly exceeding, for example that between frog and human (Johns and Avise 1998). Fish occupy virtually every aquatic habitat, from tropical reefs to abyssal depths; some have even adopted amphibian-like lifestyles. Associated ecological and behavioural demands have fashioned basic brain designs into a vast number of species-specific variations on the theme (Nieuwenhuys et al. 1998). Recent papers based on a combination of quantitative techniques and applications of phylogenetically controlled statistical designs have illuminated the characteristics of evolutionary trends in a variety of taxa. In short, both ecology and phylogenetic distance account for brain variability. For example, when comparing the brains of sharks and teleosts, effects of evolutionary history prevail, whereas nested downwards, comparisons within the latter taxon (i.e. within the cichlids or within cyprinids) increasingly pinpoint ecology as the major covariant of morphology.

6.2.1 Comparative Studies of Brain Evolution

When brains are compared between species, this is often done to relate the detected anatomical differences to functional properties. The rationale behind this is that anatomical structure is the result of the integration of the past selection pressures. We are here adhere to the broad definition of cognition, which includes perception, learning, processing, storage, and retrieval of information (Shettleworth 2010). Although challenged by some (Chittka and Niven 2009), brain size, absolute and/or relative, is often used as a proxy for cognitive ability (Striedter 2005). Evidence for this relationship comes largely from phylogenetically controlled comparative analyses. The logic of those analyses is that more closely related species are more similar than more distantly related species (Harvey and Pagel 1991). Controlling for this phylogeny effect, comparative analyses reveal macroevolutionary patterns. In birds and mammals, relative brain size and cognitive ability are positively associated (Benson-Amram et al. 2016; MacLean et al. 2014). The majority of comparative analyses in brain anatomy is done in mammals and birds, whereas studies relating brain size to cognitive abilities across species in fish are currently lacking. In Lake Tanganyika cichlids relative brain size is positively associated with social and environmental complexity (Pollen et al. 2007; van Staaden et al. 1995), but also with the type of diet (Gonzalez-Voyer et al. 2009). Sex-specific analyses in these cichlids showed that female care-type (bi-parental or female-only) determined brain size in females, but not in males. Likewise, in pipefishes and seahorses, feeding ecology and brain size seem to be linked as longer snouts (an adaptation to more mobile prey) correlate with larger brains (Tsuboi et al. 2017). The high costs of brain tissue (Kuzawa et al. 2014) likely limit brain evolution as indicated by apparent

trade-offs between brain size and other costly organs such as the gut (Lake Tanganyika cichlids, Tsuboi et al. 2014b) or fat tissue (Pacific seaweed pipefish, Tsuboi et al. 2016).

6.2.2 Brain Plasticity

Adaptive phenotypic plasticity (West-Eberhard 2003) can allow for faster adjustments to prevailing conditions than trans-generational adaptation (Ghalambor et al. 2007). In teleosts (Wagner 2003) and elasmobranchs (Lisney et al. 2007), life-stage specific habitat shifts trigger changes in size of the brain parts relevant for the respective ages. Brain plasticity is also commonly observed in experimental settings. Captive rearing changes brain anatomy in most fish species investigated so far, it affects olfactory bulb and Telencephalon size in Chinook salmon (*Oncorhynchus tshawytscha*; (Kihslinger and Nevitt 2006), brain, optic tectum, and Telencephalon size in Guppies (*Poecilia reticulata*; Burns et al. 2009), sometimes overall brain size in nine-spined stickleback (*Pungitius pungitius*; Gonda et al. 2011), and Telencephalon size in three-spined stickleback (*Gasterosteus aculeatus*; Park et al. 2012). Generally, brain and region sizes are smaller in captive-reared fishes, while environmental enrichment can counteract such effects and lead to size increases of brain regions. Enrichment increased cell proliferation in the Telencephalon of coho salmon (*Oncorhynchus kisutch*; Lema et al. 2005) and triggered the development of larger Cerebellum in steelhead trout (*Oncorhynchus mykiss*; Kihslinger and Nevitt 2006). Most fish grow indeterminately, and a major difference between the brain of fish and that of poikilothermic vertebrates is that fish brains show much more cell proliferation also as adults (Zupanc 2001), accounting for a pronounced phenotypic plasticity and adaptive potential also at later life stages. For instance, a change in social status correlates with increased cell proliferation rate in salmonids (Sørensen et al. 2007), a greater female availability boosts brain size in male guppies (Kotrschal et al. 2012b), and changes in rearing-group size change most brain regions in cichlids (Fischer et al. 2015).

6.2.3 The Brain-Size-Selected Guppies

As highlighted in Sect. 6.2.1, comparative methods are useful to unravel the macroevolutionary patterns in fish brain anatomy. However, they produce correlational results, as a causative relationship can only be established by experimental manipulation. In the following, we will summarize the findings of the first such experiments in brain evolution, done with the guppy (*Poecilia reticulata*), a small fish of the Poeciliidae that inhabits shallow streams in Trinidad and Northern Venezuela. This is a model organism in several disciplines of biology, including ecology, evolutionary biology, and behavioural biology; it was used for artificial

selection on large and small relative brain size for *experimentally* testing established concepts of brain evolution. In addition, this unique model system revealed some previously unknown costs and benefits of evolving a large brain.

The guppy brain size selection lines were generated using an artificial selection design consisting of two replicated treatments (three up-selected lines and three down-selected lines). Since brain size can only be quantified after dissection, pairs were first allowed to breed at least two clutches and then sacrificed for brain quantification. The offspring from parents with large or small relative brain size were then used for starting the next generation. More specifically, to select for *relative* brain size (controlled for body size), the residuals from the regression of brain size (weight) on body size (length) of both parents were used. Three times 75 pairs (75 pairs per replicate) were started to create the first three "up" and "down" selected lines (six lines in total). Male and female residuals for each pair were summed and the offspring from the top and bottom 25% of these "parental residuals" were used to form the next-generation parental groups. Then offspring of the 30 pairs with the largest residual sums for up-selection and the 30 pairs with the smallest residual sums for down-selection were propagated for each of the following generations. Already the second generation showed a 9% difference in relative brain size between lines and the third differed by up to 14%, at unchanged body size. The larger brains were composed of more neurons (Marhounová et al. 2019), but the 11 main brain regions remained proportionally similar between the lines (Kotrschal et al. 2017). These large- and small-brained lines were compared in a range of traits to determine the costs and benefits of large brain size.

As described above a relatively larger brain seems to confer a cognitive benefit (Benson-Amram et al. 2016; MacLean et al. 2014). This was indeed the case in several tests of learning and memory in the brain size lines. For instance, using food as a reward, large-brained females were better at numerical learning (Kotrschal et al. 2013) and outperformed small-brained females in a reversal-learning test (Buechel et al. 2018). Large-brained males, in turn, were better at learning and memorizing the way through a maze when a virgin female was the reward (Kotrschal et al. 2014a). But is this simply an "academic" difference in cognitive performance or does an increase in cognitive ability matter in the life of a guppy? To test this, six large semi-natural streams were stocked with 800 guppies each (balanced over sex and brain size selection line and individually marked using green and red elastomer implants), and one pike cichlid (*Crenicichla alta*), a natural guppy predator from Trinidad, was introduced into each of those streams. In weekly censuses survival of fish was monitored and showed that large-brained females survived longer and in greater numbers (Kotrschal et al. 2015a). After 14 weeks exactly half of the large-brained females, but only 44.5% of the small-brained females were still alive. Males were eaten faster than females, but the large- and small-brained males did not differ in survival. These findings provoked two questions: Why did the large-brained females survive better and why did the large-brained males not benefit from a larger brain?

The improved survival of large- over small-brained females was likely due to their cognitive advantages that enabled them to better avoid predation. The pike cichlids sat hidden in the deepest part of the streams, striking at fish passing

by. Better learning and memory should help learning about and avoiding those dangerous areas of the stream. Guppies show predator inspection (Dugatkin and Godin 1992). A change in cognitive ability may impact this behaviour in several ways and indeed, a follow-up experiment showed that larger-brained animals seem to be faster at gathering and integrating information about the predator's state because they inspected for a shorter time and also from further away (van der Bijl et al. 2015). But why did the large-brained males not show a survival advantage over small-brained males? After all, they also show predator inspection and are known to outperform small-brained males in tests of learning and memory. Potentially because large-brained males in these selection lines are more colourful than the small-brained males (Kotrschal et al. 2015c); it is still not understood why, but it is likely due to a genetic correlation between brain size and coloration. Large-brained guppy males had larger orange and iridescent spots. Pike cichlids are visual hunters with a known preference for more colourful individuals (Endler 1980). Therefore, the large-brained males' increased conspicuousness may have overridden the cognitive benefits of a larger brain.

So, a larger brain confers several benefits, related to cognition and survival. Large-brained males also seem to have a mating advantage as several traits that are known to be beneficial during mating are exaggerated in large-brained males aside the already mentioned colourfulness. They also have a longer tail fin, a known trait relevant for female choice, and also a longer gonopodium (Kotrschal et al. 2015c), which is the anal fin modified to function as intromittent organ. Guppy males often sneak up on females and attempt to mate coercively and a longer gonopodium facilitates such copulations (Houde 1987). However, several tests of mate choice did not reveal any significant mating advantage of large- over small-brained males (unpublished data). In females, brain size may also be relevant during mating, because accurate assessment of partner quality may depend on cognitive ability (Verzijden et al. 2012). Indeed, when given the choice between very colourful and less colourful males, large-brained females showed a more pronounced preference for the attractive than for the less-attractive male (Corral-Lopez et al. 2017). In contrast, small-brained and wild-type females showed no preference. In-depth analysis of optomotor response to colour cues and gene expression of opsins in the eye revealed that the observed differences were not due to differences in visual perception of colour or visual acuity (Corral-López et al. 2017), indicating that differences in the ability to process indicators of attractiveness are responsible. While brain size did not impact general sexual behaviour (Corral-López et al. 2015) in males, it did effect context-specific mate choice as large-brained males could better discriminate between differentially-sized females (Corral-López et al. 2018).

Are small-brained guppies simply "sub-optimal" guppies? This may appear so at first since they seem to be inferior to large-brained animals in so many traits. But this is probably not the case, because several classic indicators of quality showed no difference between large- and small-brained animals; those include body condition, swimming endurance, escape velocity ("C-start"), and adult body size (Kotrschal et al. 2014b). Several traits were, in fact, more prominent in small- compared to large-brained guppies indicating that costs are associated with developing a larger

brain. For instance, in their first parturition, small-brained guppy females gave birth to 15% more offspring compared to large-brained females (Kotrschal et al. 2013). This indicates a trade-off between investment in brain size or fecundity. Further indications of trade-offs include a decreased innate (but not acquired) immune response in large-brained animals (Kotrschal et al. 2016), a slower juvenile speed of growth in large-brained animals (Kotrschal et al. 2015b), a smaller gut size in large-brained animals (Kotrschal et al. 2013), but slower intrinsic ageing in small-brained animals (Kotrschal et al. 2019).

In summary, three generations of artificial selection on relative brain size lead to up to 14% difference in brain size between guppies selected for large and small brains. A larger brain confers cognitive benefits as the large-brained animals outperformed the small-brained animals in several tests of learning and memory. A larger brain also seems beneficial for female mate choice, male attractiveness, and for anti-predator behaviour and survival. However, evolving a larger brain comes at some costs. Large-brained animals showed a decreased fecundity, smaller guts, slower juvenile growth rate, impaired immunity, and faster ageing. It is conceivable that guppies selected for different brain sizes may also slightly differ in their habitat preferences and requirements. However, no tests regarding habitat preferences as related to brain size have hitherto be conducted, rendering any conclusions regarding brain size-related welfare requirements speculative.

References

Allis EP (1897) The cranial muscles and cranial and first spinal nerves in *Amia calva*, vol 12. Ginn & Company, p 487

Benson-Amram S, Dantzer B, Stricker G, Swanson EM, Holekamp KE (2016) Brain size predicts problem-solving ability in mammalian carnivores. Proc Natl Acad Sci U S A 113(9):2532–2537

Bone Q (1977) Mauthner neurons in elasmobranchs. J Mar Biol Assoc U K 57:253–259

Bone Q, Marshal NB, Blaxter LHS (1982) Biology of fishes. Chapman & Hall, London

Brandstatter R, Kotrschal K (1990) Brain growth-patterns in 4 European cyprinid fish species (Cyprinidae, Teleostei) – roach (*Rutilus-rutilus*), bream (*Abramis-brama*), common carp (*Cyprinus-carpio*) and sabre carp (*Pelecus-cultratus*). Brain Behav Evol 35:195–211

Buechel SD, Boussard A, Kotrschal A, van der Bijl W, Kolm N (2018) Brain size affects performance in a reversal-learning test. Proc R Soc B 285:20172031

Burns JG, Saravanan A, Rodd FH (2009) Rearing environment affects the brain size of guppies: lab-reared guppies have smaller brains than wild-caught guppies. Ethology 115:122–133

Chittka L, Niven J (2009) Are bigger brains better? Curr Biol 19:R995–R1008

Corral-López A, Eckerström-Liedholm S, Der Bijl WV, Kotrschal A, Kolm N (2015) No association between brain size and male sexual behavior in the guppy. Curr Zool 61:265–273

Corral-Lopez A, Bloch N, Kotrschal A, van der Bijl W, Buechel S, Mank JE, Kolm N (2017) Female brain size affects the assessment of male attractiveness during mate choice. Sci Adv 3: e1601990

Corral-López A, Garate-Olaizola M, Buechel SD, Kolm N, Kotrschal A (2017) On the role of body size, brain size, and eye size in visual acuity. Behav Ecol Sociobiol 71:179

Corral-López A, Kotrschal A, Kolm N (2018) Selection for relative brain size affects context-dependent male preferences, but not discrimination, of female body size in guppies. J Exp Biol. https://doi.org/10.1242/jeb.175240

Costa SS, Andrade R, Carneiro LA, Gonçalves EJ, Kotrschal K, Oliveira RF (2011) Sex differences in the dorsolateral telencephalon correlate with home range size in blenniid fish. Brain Behav Evol 77:55–64

Davis R, Northcutt R (1983) Fish neurobiology, vol 2, Higher brain areas and functions. University of Michigan Press, Ann Arbor, MI

Dugatkin LA, Godin JGJ (1992) Predator inspection, shoaling and foraging under predation Hazard in the Trinidadian guppy, *Poecilia-reticulata*. Environ Biol Fish 34:265–276

Endler JA (1980) Natural-selection on color patterns in *Poecilia-reticulata*. Evolution 34:76–91

Finger TE (1980) Nonolfactory sensory pathway to the telencephalon in a teleost fish. Science 210:671–673

Fischer S, Bessert-Nettelbeck M, Kotrschal A, Taborsky B (2015) Rearing-group size determines social competence and brain structure in a cooperatively breeding cichlid. Am Nat 186:123

Ghalambor CK, McKay JK, Carroll SP, Reznick DN (2007) Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. Funct Ecol 21:394–407

Gonda A, Herczeg G, Merila J (2011) Population variation in brain size of nine-spined sticklebacks (*Pungitius pungitius*) – local adaptation or environmentally induced variation? BMC Evol Biol 11:75

Gonzalez-Voyer A, Winberg S, Kolm N (2009) Social fishes and single mothers: brain evolution in African cichlids. Proc R Soc B Biol Sci 276:161–167

Harvey PH, Pagel MD (1991) The comparative method in evolutionary biology. Oxford University Press, Oxford

Herculano-Houzel S (2009) The human brain in numbers: a linearly scaled-up primate brain. Front Hum Neurosci 3:31

Herrick CJ (1902) A note on the significance of the size of nerve fibers in fishes. J Comp Neurol 12 (4):329–334

Herrick CJ (1906) On the centers for taste and touch in the medulla oblongata of fishes. J Comp Neurol Psychol 16(6):403–439

Houde AE (1987) Mate choice based upon naturally-occurring color-pattern variation in a guppy population. Evolution 41:1–10

Johns GC, Avise JC (1998) A comparative summary of genetic distances in the vertebrates from the mitochondrial cytochrome b gene. Mol Biol Evol 15:1481–1490

Kanwal JS, Finger TE (1992) Central representation and projections of gustatory systems. In: Hara TJ (ed) Fish chemoreception. Springer, pp 79–102

Kihslinger RL, Nevitt GA (2006) Early rearing environment impacts cerebellar growth in juvenile salmon. J Exp Biol 209:504–509

Kotrschal A, Taborsky B (2010) Resource defence or exploded lek?–a question of perspective. Ethology 116:1189–1198

Kotrschal K, Adam H, Brandstätter R, Junger H, Zaunreiter M, Goldschmid A (1990) Larval size constraints determine directional ontogenetic shifts in the visual system of teleosts. J Zool Syst Evol Res 28:166–182

Kotrschal K, van Staaden MJ, Huber R (1998) Fish brains: evolution and environmental relationships. Rev Fish Biol Fish 8:373–408

Kotrschal A, Heckel G, Bonfils D, Taborsky B (2012a) Life-stage specific environments in a cichlid fish: implications for inducible maternal effects. Evol Ecol 26:123–137

Kotrschal A, Rogell B, Maklakov AA, Kolm N (2012b) Sex-specific plasticity in brain morphology depends on social environment of the guppy, *Poecilia reticulata*. Behav Ecol Sociobiol 66:1485–1492

Kotrschal A, Rogell B, Bundsen A, Svensson B, Zajitschek S, Brännström I, Immler S, Maklakov AA, Kolm N (2013) Artificial selection on relative brain size in the guppy reveals costs and benefits of evolving a larger brain. Curr Biol 23:168–171

Kotrschal A, Corral-Lopez A, Amcoff M, Kolm N (2014a) A larger brain confers a benefit in a spatial mate search learning task in male guppies. Behav Ecol 26:527–532

Kotrschal A, Lievens EJ, Dahlbom J, Bundsen A, Semenova S, Sundvik M, Maklakov AA, Winberg S, Panula P, Kolm N (2014b) Artificial selection on relative brain size reveals a positive genetic correlation between brain size and proactive personality in the guppy. Evolution 68:1139–1149

Kotrschal A, Buechel S, Zala S, Corral Lopez A, Penn DJ, Kolm N (2015a) Brain size affects female but not male survival under predation threat. Ecol Lett 18:646–652

Kotrschal A, Corral-Lopez A, Szidat S, Kolm N (2015b) The effect of brain size evolution on feeding propensity, digestive efficiency, and juvenile growth. Evolution 69:3013–3020

Kotrschal A, Corral-Lopez A, Zajitschek S, Immler S, Maklakov AA, Kolm N (2015c) Positive genetic correlation between brain size and sexual traits in male guppies artificially selected for brain size. J Evol Biol 28:841–850

Kotrschal A, Kolm N, Penn DJ (2016) Selection for brain size impairs innate, but not adaptive immune responses. Proc R Soc B 283:20152857

Kotrschal A, Zeng HL, van der Bijl W, Öhman-Mägi C, Kotrschal K, Pelckmans K, Kolm N (2017) Evolution of brain region volumes during artificial selection for relative brain size. Evolution 71:2942–2951

Kotrschal A, Corral-Lopez A, Kolm N (2019) Large brains, short life: selection on brain size impacts intrinsic lifespan. Biol Lett 15:20190137

Kruska DC (1988) The brain of the basking shark (Cetorhinus maximus). Brain Behav Evol 32 (6):353–363

Kuzawa CW, Chugani HT, Grossman LI, Lipovich L, Muzik O, Hof PR, Wildman DE, Sherwood CC, Leonard WR, Lange N (2014) Metabolic costs and evolutionary implications of human brain development. Proc Natl Acad Sci U S A 111:13010–13015

Lema SC, Hodges MJ, Marchetti MP, Nevitt GA (2005) Proliferation zones in the salmon telencephalon and evidence for environmental influence on proliferation rate. Comp Biochem Physiol A Mol Integr Physiol 141:327–335

Lisney TJ, Bennett MB, Collin SP (2007) Volumetric analysis of sensory brain areas indicates ontogenetic shifts in the relative importance of sensory systems in elasmobranchs. Raffles Bull Zool 14:7–15

MacLean EL, Hare B, Nunn CL, Addessi E, Amici F, Anderson RC, Aureli F, Baker JM, Bania AE, Barnard AM, Boogert NJ, Brannon EM, Bray EE, Bray J, Brent LJN, Burkart JM, Call J, Cantlon JF, Cheke LG, Clayton NS, Delgado MM, DiVincenti LJ, Fujita K, Herrmann E, Hiramatsu C, Jacobs LF, Jordan KE, Laude JR, Leimgruber KL, Messer EJE, de A. Moura AC, Ostojiƒá L, Picard A, Platt ML, Plotnik JM, Range F, Reader SM, Reddy RB, Sandel AA, Santos LR, Schumann K, Seed AM, Sewall KB, Shaw RC, Slocombe KE, Su Y, Takimoto A, Tan J, Tao R, van Schaik CP, Viranyi Z, Visalberghi E, Wade JC, Watanabe A, Widness J, Young JK, Zentall TR, Zhao Y (2014) The evolution of self-control. Proc Natl Acad Sci U S A 111:E2140–E2148

Maler L, Sas E, Johnston S, Ellis W (1991) An atlas of the brain of the electric fish *Apteronotus leptorhynchus*. J Chem Neuroanat 4:1–38

Marhounová L, Kotrschal A, Kverková K, Kolm N, Němec P (2019) Artificial selection on brain size leads to matching changes in overall number of neurons. Evolution 73(9):2003–2012

Mills SM (1932) The double innervation of fish melanophores. J Exp Zool A Ecol Genet Physiol 64:231–244

Nakane Y, Ikegami K, Iigo M, Ono H, Takeda K, Takahashi D, Uesaka M, Kimijima M, Hashimoto R, Arai N (2013) The saccus vasculosus of fish is a sensor of seasonal changes in day length. Nat Commun 4:2018

Nieuwenhuys R (1982) An overview of the organization of the brain of actinopterygian fishes. Am Zool 22:287–310

Nieuwenhuys R, ten Donkelaar HJ, Nicholson C (1998) The central nervous system of vertebrates. Springer, Heidelberg

Northcutt RG (1978) Brain organization in the cartilaginous fishes. In: Hodgson ES, Mathewson RF (eds) Sensory biology of sharks, skates and rays. Office of Naval Research, Washington, DC, pp 117–193

Northcutt RG, Davis R (1983) Fish neurobiology: brain stem and sense organs. University of Michigan Press, Ann Arbor, MI

Okuyama T, Yokoi S, Abe H, Isoe Y, Suehiro Y, Imada H, Tanaka M, Kawasaki T, Yuba S, Taniguchi Y (2014) A neural mechanism underlying mating preferences for familiar individuals in medaka fish. Science 343:91–94

Östlund-Nilsson S, Mayer I, Huntingford FA (2007) Biology of the three-spined stickleback. CRC Press, Boca Raton, FL

Park PJ, Chase I, Bell MA (2012) Phenotypic plasticity of the threespine stickleback *Gasterosteus aculeatus* telencephalon in response to experience in captivity. Curr Zool 58:189–210

Pollen AA, Dobberfuhl AP, Scace J, Igulu MM, Renn SCP, Shumway CA, Hofmann HA (2007) Environmental complexity and social organization sculpt the brain in Lake Tanganyikan cichlid fish. Brain Behav Evol 70:21–39

Popper AN, Fay RR (1993) Sound detection and processing by fish: critical review and major research questions (part 1 of 2). Brain Behav Evol 41:14–25

Portavella M, Vargas J, Torres B, Salas C (2002) The effects of telencephalic pallial lesions on spatial, temporal, and emotional learning in goldfish. Brain Res Bull 57:397–399

Puelles L, Harrison M, Paxinos G, Watson C (2013) A developmental ontology for the mammalian brain based on the prosomeric model. Trends Neurosci 36:570–578

Rodríguez F, Durán E, Gomez A, Ocana F, Alvarez E, Jiménez-Moya F, Broglio C, Salas C (2005) Cognitive and emotional functions of the teleost fish cerebellum. Brain Res Bull 66:365–370

Salas C, Broglio C, Durán E, Gómez A, Ocaña FM, Jiménez-Moya F, Rodríguez F (2006) Neuropsychology of learning and memory in teleost fish. Zebrafish 3:157–171

Schellart NA (1991) Interrelations between the auditory, the visual and the lateral line systems of teleosts; a mini-review of modelling sensory capabilities. Neth J Zool 42:459–477

Shettleworth SJ (2010) Cognition, evolution, and behavior, 2nd edn. Oxford University Press, Oxford

Sibbing F (1991) Food capture and oral processing. In: Nelson J, Winfield IJ (eds) Cyprinid fishes. Springer, pp 377–412

Sørensen C, Øverli Ø, Summers CH, Nilsson GE (2007) Social regulation of neurogenesis in teleosts. Brain Behav Evol 70:239–246

Striedter GF (2005) Principles of brain evolution. Sinauer Associates, Sunderland

Szabó I (1973) Path neuron system of medial forebrain bundle as a possible substrate for hypothalamic self-stimulation. Physiol Behav 10:315–328

Tinbergen N (1951) The study of instinct. Oxford University Press, New York

Tsuboi M, Gonzalez-Voyer A, Kolm N (2014a) Phenotypic integration of brain size and head morphology in Lake Tanganyika Cichlids. BMC Evol Biol 14:39

Tsuboi M, Husby A, Kotrschal A, Hayward A, Buechel S, Zidar J, Lovle H, Kolm N (2014b) Comparative support for the expensive tissue hypothesis: big brains are correlated with smaller gut and greater parental investment in Lake Tanganyika cichlids. Evolution 69:190–200

Tsuboi M, Shoji J, Sogabe A, Ahnesjö I, Kolm N (2016) Within species support for the expensive tissue hypothesis: a negative association between brain size and visceral fat storage in females of the Pacific seaweed pipefish. Ecol Evol 6:647–655

Tsuboi M, Lim ACO, Ooi BL, Yip MY, Chong VC, Ahnesjö I, Kolm N (2017) Brain size evolution in pipefishes and seahorses: the role of feeding ecology, life history and sexual selection. J Evol Biol 30:150–160

van der Bijl W, Thyselius M, Kotrschal A, Kolm N (2015) Brain size affects the behavioral response to predators in female guppies (*Poecilia reticulata*). Proc R Soc B Biol Sci 282:20151132

van Staaden MJ, Huber R, Kaufmann LS, Liem KF (1995) Brain evolution in cichlids of the African Great Lakes: brain and body size, general patterns and evolutionary trends. Zoology 98:165–178

Vanegas H, Ito H (1983) Morphological aspects of the teleostean visual system: a review. Brain Res Rev 6:117–137

Verzijden MN, Ten Cate C, Servedio MR, Kozak GM, Boughman JW, Svensson EI (2012) The impact of learning on sexual selection and speciation. Trends Ecol Evol 27:511–519

Von Kupffer C (1891) The development of the cranial nerves of vertebrates. J Comp Neurol 1:246–264

Voneida TJ, Fish SE (1984) Central nervous system changes related to the reduction of visual input in a naturally blind fish (*Astyanax hubbsi*). Am Zool 24:775–782

Wagner H-J (2003) Volumetric analysis of brain areas indicates a shift in sensory orientation during development in the deep-sea grenadier *Coryphaenoides armatus*. Mar Biol 142:791–797

Webb J, Northcutt R (1997) Morphology and distribution of pit organs and canal neuromasts in non-teleost bony fishes. Brain Behav Evol 50:139–151

Weiger T, Lametschwandtner A, Kotrschal K, Krautgartner WD (1988) Vascularization of the telencephalic choroid plexus of a ganoid fish [*Acipenser ruthenus* (L.)]. Dev Dyn 182:33–41

West-Eberhard M (2003) Developmental plasticity and evolution. Oxford University Press, Oxford

Wullimann MF (1994) The teleostean torus longitudinalis. Eur J Morphol 32:235–242

Young JZ (1931) Memoirs: on the autonomic nervous system of the teleostean fish *Uranoscopus scaber*. J Cell Sci 2:491–536

Young J (1980) Nervous control of gut movements in Lophius. J Mar Biol Assoc U K 60:19–30

Zaunreiter M, Kotrschal K, Goldschmid A, Adam H (1985) Ecomorphology of the optic system in 5 species of blennies (Teleostei). Fortschr Zool 30:731–734

Zupanc GKH (2001) Adult neurogenesis and neuronal regeneration in the central nervous system of teleost fish. Brain Behav Evol 58:250–275